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OPTIMIZATION OF THE CURRENT BREEDING SCHEME FOR BLUE FOX

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ACADEMIC DISSERTATION

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ABSTRACT

Finland is a leading blue fox pelt producer globally. Approximately every second blue fox pelt in the world is produced in Finland. The mean size of blue fox pelts has increased rapidly during the last 20 years. Over the same period, the mean litter result (number of pups born per mated female) has decreased. Poor fertility is especially a problem of young females. The goals of Finnish blue fox production are to increase pelt size, improve pelt quality and increase the litter result. Breeding values are estimated for litter size and for pelt size, quality, color darkness (scale from white to black) and color clarity (scale from red to blue). Two separate approaches to characterize pelt traits are in use: grading of live animals and evaluation of pelts in the auction house. The pelt traits, such as size, quality and color darkness and clarity are first graded on live animals (grading traits) and later after slaughtering evaluated on processed pelts displayed for auction sales (pelt character traits).

The study was divided into three parts. The first part was to estimate state of variation. The second part estimated genetic (co)variation for pelt traits and litter size. The third part used bio-economic modeling to estimate economic weights in Finnish blue fox production and compared different selection strategies from an economic point of view.

Finnish blue fox population has relatively large effective population size and inbreeding is not a problem in the Finnish blue fox population.

The heritabilities of the traits in Finnish blue fox breeding vary from 6-10% for fertility traits and 10-55% for pelt traits. The highest heritability was found for color darkness and the lowest for litter size. Among traits that are easy to measure such as animal size, pelt size and color darkness, the genetic correlation between live animal grading and pelt grading was high. Color clarity is a difficult trait to measure under farm conditions. Genetic correlation between pelt color clarity and grading color clarity was low. Pelt size and animal size have antagonistic genetic correlation with litter size.

Fertility and pelt quality are the most economically valuable traits in Finnish blue fox production. The selection based on litter size, grading traits and pelt character traits gave only slightly better economic results than selection based on only pelt character traits and on litter size. Using the grading traits gave a poorer economic outcome than pelt traits. The selection of breeding candidates while restricting genetic change in pelt size to zero caused only minor losses in economic results.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications:

- I Strandén, I. & Peura, J. 2007. Inbreeding and relationship coefficients in the Finnish blue fox population. *Agricultural and Food Science*, 16: 147-156
- II Peura, J., Strandén, I. & Mäntysaari, E.A. 2007. Genetic parameters for Finnish blue fox population: litter size, age at first insemination and pelt size. *Agricultural and Food Science*, 16: 136-146
- III Peura, J., Strandén, I. & Mäntysaari, E.A. 2005. Genetic parameters in Finnish blue fox population: Pelt character and live animal grading traits. *Acta Agriculturae Scandinavica, Section A, Animal Science*, 55:137-144
- IV Peura, J., Strandén, I. & Mäntysaari, E.A. 2013. Profitable blue fox production: economic values for Finnish blue fox. *Acta Agriculturae Scandinavica, Section A, Animal Science*, DOI:10.1080/09064702.2013.789547

Contribution of the author to papers I to IV:

- I.** The author participated in the planning of the study, participated in preparing the data for statistical analyses, participated in interpreting the results and participated in writing.
- II.** The author participated in the planning of the study, conducted the statistical analyses, interpreted the results and was the main writer of paper II.
- III.** The author participated in the planning of the study, conducted the statistical analyses, interpreted the results and was the main writer of paper III.
- IV.** The author participated in the planning of the study, conducted the statistical analyses, interpreted the results and was the main writer of paper IV

1 INTRODUCTION

1.1 FINNISH BLUE FOX PRODUCTION

1.1.1 FUR MARKETS

Mink and foxes (Blue fox and red fox) are most important fur producing animals in the world. Annual global production is approximately 53 million mink pelts and 3.7 million fox pelts. The most important mink producers are Denmark (15 million) and China (13.5 million).

Finland produces the highest number of blue fox pelts in the world. In Finland there are approximately 1000 fur farms with a mean production of 1400 pelts per year per farm (Saga Furs, 2012). During the season of 2009-2010 Finnish fox farms produced 1.7 million fox pelts, which is approximately 46% of the global fox pelt production. The biggest buyers of Finnish blue fox pelts are Hong Kong (43%), the United Kingdom (11%) and China (7%). The total value of 2011 sales of Saga Furs Oyj was 650 million Euros. Other globally important fur trading companies are north-American American Legend Coop., North American Fur Auctions and Fur Harvesters Auction inc., Danish Copenhagen Fur and Russian Sojuzpushnina EEA.

Fur animal production differs from other animal production especially in the pricing system of the final product. Most Finnish blue fox pelts are sold via fur auctions of Saga Furs Oyj. Fur is a luxury product and, therefore, global fashion trends greatly affect the mean price of pelts. The mean price of a similar quality and size of pelt may be very different from year even after adjustment for inflation. Finnish fur animal production has never received government production subsidies (based on the number of animals) unlike other farm animal production systems.

1.1.2 GRADING OF PELTS

There are several factors that affect the price of a pelt. Certain coat color types are more popular than others. Global fashion trends especially determine which color types are the most popular for any season. Often the price of the color types most in demand is high. This leads to the increased production of popular the color type in the next year. Because of the higher supply of the popular color types, their price usually decreases within 1-2 years after the price peak.

The main factors that affect pelt prices are size and quality of pelt. Pelt quality depends on several factors, the most important being under fur and guard hair quality and their reciprocal association.

Pelts are graded into homogenous groups by professional graders according to their size, color and quality. Grading ensures a large assortment for the buyer.

Saga Furs Oyj has 22 commercial color types one of which is matched to each pelt during the sorting process. Within the color type class, each pelt is further sorted into sub-classes by the size, color darkness, color clarity and quality. Pelt size is measured by an automatic sorting machine that measures pelt length and classifies each pelt into the correct size group. Currently there are 6 size groups (Figure 1) for foxes. The difference between each size group is 9 cm. All pelts longer than 133 cm are sorted into group 50.



Figure 1. The Saga Furs size sorting system: each pelt is sorted by its length to size group 1, 0, 20, 30, 40 or 50. Figure: Saga Furs Oyj

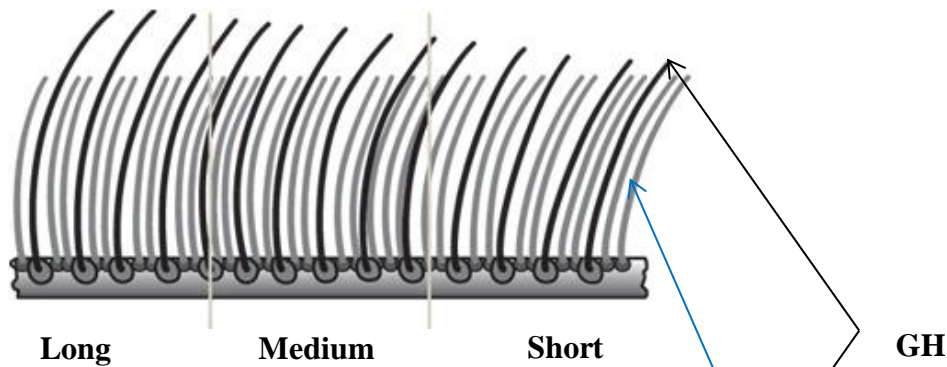


Figure 2. Color clarity scale from blue (I) to red (IV). Figure: Saga Furs Oyj

Color darkness is measured by another automatic sorting machine. Each pelt is sorted and allocated to one of 11 color darkness groups (3Xdark, 2Xdark, Xdark, dark, medium, Pale, Xpale, 2Xpale, 3Xpale, 4Xpale and white). Color clarity has four classes (Figure 2) with a scale that ranges from blue to red.

Fur quality is a complex trait. Each pelt is classified according to its quality by professional graders. The grader takes into account several factors that affect quality of the pelt. First the pelts are divided into high quality SAGA-classes (SAGA and SAGA I) and lower quality low grades (IA, IB and II). Second, within SAGA classes each pelt is graded by the quality of guard hair and under fur (Figure 3).

GUARD HAIR QUALITY



UNDER FUR QUALITY

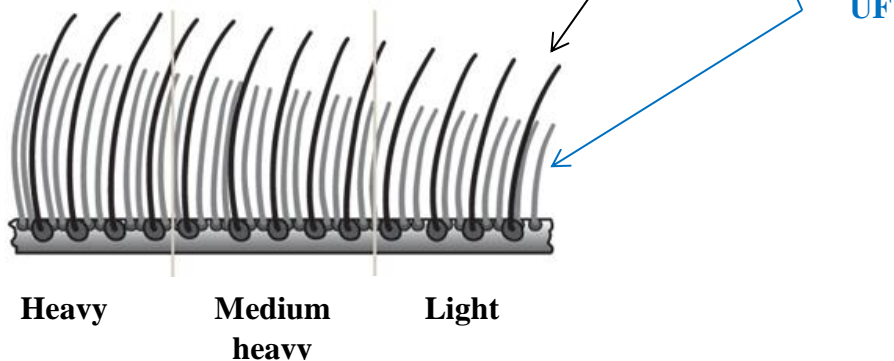


Figure 3. Fox fur has two layers of fur, longer and stronger guard hair (GH) and shorter and softer under fur (UF).

For breeding purposes, auction house scales for pelt size, quality, color darkness and clarity are transformed into a scale that ranges from 1 to 5 (Table 1).

Table 1. *Classes of pelt traits used in the auction house and in the Finnish breeding scheme*

Class in the analysis for traits	Corresponding classes in the auction house sorting system			
	Size cm	Darkness ¹⁾	Clarity ²⁾	Quality ³⁾
1	< 106.1	XXXXPale-XPale	OC-	-
2	106.1-115	Pale	OC	II
3	115.1-124	Medium	R-	IA-IB
4	124.1-133	Dark	R	Saga
5	> 133	Xdark-Black	R+	SagaRoyal

¹⁾Color scale from lightest (XXXXPale) to darkest (Black)

²⁾The scale from OC- off color to R+ corresponds clarity of blue color

³⁾SagaRoyal is the best quality and II is the poorest quality.

1.1.3 FERTILITY OF BLUE FOXES

The mean size of blue fox pelts has increased rapidly during the last 20 years. Pelt size, animal size and fatness of the blue fox are highly correlated traits (Rekilä et al. 2000; Kempe et al. 2009).

Under natural conditions, the arctic fox lives in the arctic. In areas where survival of the fox depends highly on the animal's ability to store energy as fat during late summer and autumn for winter to be able to survive during the lean winter months (Prestrud & Nilssen 1992). It is likely that arctic foxes with best survival ability have a good capacity to store fat during the autumn. According to Kempe et al. (2009) fatness of blue fox has moderate heritability. However, in farming conditions, fatness has also antagonistic genetic correlation with leg weakness (Kempe et al. 2010) and with fertility (Koivula et al. 2009).

The profit for the fur farmer is not determined only by pelt size, quality and color type. One of the most important factors affecting the farmer's profit is the number of pelts produced per breeding female, i.e. mean litter size (Figure 4) and the dam's ability to keep her pups alive to produce pelts. The blue fox is a seasonal breeder by which the blue fox comes into heat only once a year. The mating season of blue foxes occurs over April and May. The mean litter size of the blue fox is 6-7 pups (Peura 2004; Koivula et al. 2009), and the first litter size is usually smaller than the second and subsequent litters.

The most important fertility trait is the litter result (pups born per mated female). This takes into account barren females and females that have lost their pups for one reason or another.

The mean litter result has been decreasing in Finnish fox farms for many years. The proportion of barren females have increased and mean litter size / litter have decreased (Bengts 2008). Pregnancy rate is a proportion of barren females (Koivula et al. 2009). In the study by Peura (2004) approximately 20% of young females were barren. In the study by Koivula et al. (2009) proportion of barren young females was reported to be 16%.

Felicity (Koivula et al. 2009) is the proportion of young non-barren females, which lost their pups before pups reached three weeks of age. In the study by Peura (2004) felicity was found to be 20% and the study by Koivula et al. (2009) it was 19%. According to Peura (2004) felicity was 10% among older females.

It is common that young females have lower fertility levels than older females. Similar findings have also been made for mink (Koivula et al. 2008) and swine (Serenius et al. 2003).

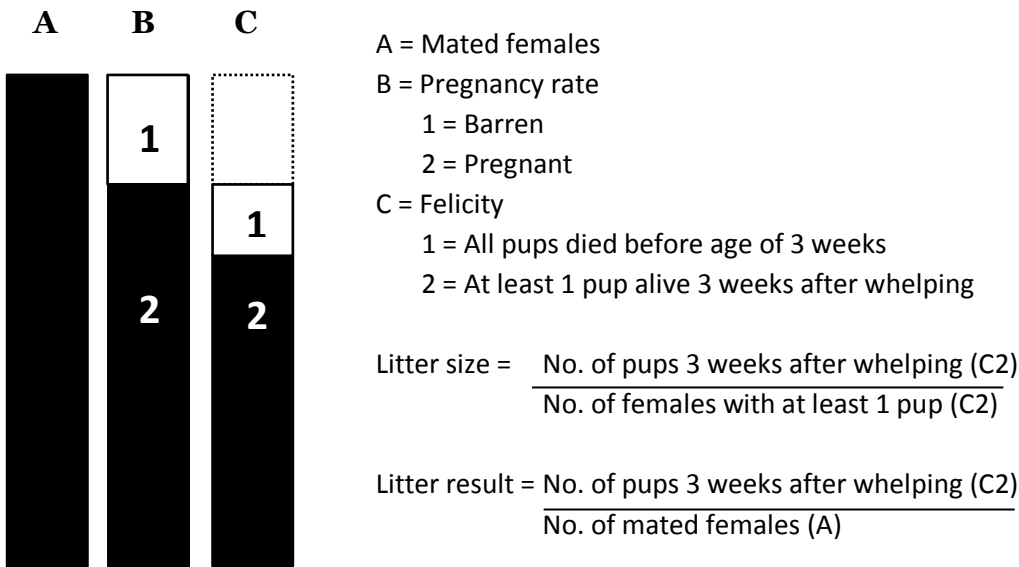


Figure 4. Fertility traits in Finnish blue fox breeding scheme

1.2 CURRENT BREEDING SCHEME OF FINNISH BLUE FOX PRODUCTION

The main breeding goals in Finnish blue fox production are to increase the pelt size, improve pelt quality and increase the litter result. However, pelt traits can be measured only from culled animals. Moreover, these animals cannot be parents to the next generation. The traits used in the Finnish blue fox breeding scheme are shown in Table 2.

Because pelt character traits can be measured only from pelted skins, farmers have developed a grading system for live animals to select as breeding animals with the best fur quality. The blue fox has two pelage seasons. In summer the fur is dark and during winter the fur is light. When the winter coat fur starts to change to summer fur, the change progresses from head to tail whereas in autumn the change occurs in the opposite direction. Day length has a major effect on the melatonin secreted, which subsequently affects the development of winter fur (Mäntysalo & Blomstedt 1995).

Table 2. *Traits in the Finnish blue fox breeding program*

Live animal grading traits	Pelt character traits	Fertility traits
Animal size	Pelt size	1 st Litter size
Grading color darkness	Pelt color darkness	2 nd + Litter size ¹
Grading color clarity	Pelt color clarity	Pregnancy
Grading density	Pelt quality	Felicity
Grading guard hair coverage		
Grading quality		

¹Repeatability model

Winter fur growth starts with the growth of guard hair. Growth of the under fur starts later in autumn. The pelt is ready for pelting, when the combination of under fur and guard hair is optimum. When the pelt is ready, pigment from the skin will have migrated into the hair follicle and the skin will have become light as a consequence. Moreover, the base of the hair follicles will be light.

Live animal grading is usually done by the farmer. Most farmers do grading 1-3 times during the autumn but the final selection is carried out very close to pelting when the fur is ready. The most important live animal grading traits are density and guard hair coverage. The goal in the selection of these traits is to improve pelt quality (Figure 3).

The pelt grading density is mainly based on a selection of under fur density. Grading of the density is achieved by palpation of the fur. It is a subjective measurement with a scale from 1 to 5, where 5 is the thickest fur. Good guard hair coverage indicates that guard hairs are evenly spaced and evenly sized and there are plenty of them. Guard hairs should be longer than under fur hairs. However, neither density nor guard hair coverage are exactly synonymous with pelt quality. Too intensive selection of either one of them may even degrade the pelt quality. Genetic correlations between grading density, grading guard hair coverage and pelt quality are not well known.

Usually live animal grading also includes color clarity and color darkness. However, color clarity is a very difficult trait to evaluate under farm

conditions. In practice, color darkness has been discovered to be very heritable. Usually strong selection pressure for color darkness is avoided because the selection can change color darkness very quickly in a population.

In Finland, most blue foxes are inseminated using artificial insemination. Consequently, some superior male can be widely used. However, most males are used only within one farm and there are no centralized male stations as for in pork or dairy production. The main reason is that the blue fox is a seasonal breeder with a relatively short mating season. It would be logistically and economically challenging to establish large-scale national semen collection and delivery centers for such a short period. Moreover, the number of semen doses collected per male would be small due to the short mating season.

Most males are used only within one farm therefore genetic links between farms are often limited. Furthermore, very little is known about the level of coefficient of inbreeding and relationship in the Finnish blue fox population. The general opinion in cattle and swine breeding is that the genetic variation is at a good level, when effective population size is above the 50 to 100 range. However, there are no studies about the effective population size in the Finnish blue fox population.

Very little is known about how traits in a breeding scheme should be weighted in Finnish conditions. According to Lohi (2002) and Lind and Lohi (1999) pelt size is the most important factor that affects pelt price. According to Wierzbicki et al. (2007) the highest economic weight should be given to litter size and fur quality. No studies have been made about economic weights in Finnish blue fox production.

No study has been made to compare different selection strategies. If selection of the quality traits is based on grading traits, the measurements are available from the breeding candidates. However, selection based on grading traits is indirect selection because the actual goal is to improve pelt character traits.

On the other hand, when selection of the breeding candidates is based on pelt character traits, none of the breeding candidates have measurements from these traits. In such cases the selection is based on pedigree information from relatives with actual measurements. Currently the farmer can choose which strategy he wants to use within his farm. At the moment, a combination that includes both the grading traits and pelt character traits is not available.

Currently, pelt size has a relatively high weight in practical selection work. Moreover, there has been concerned discussion among farmers and fur traders about the increased size of foxes. The general opinion of the auction house is that blue fox size should not be increased anymore. However, no studies have been made to ascertain if this really is the most economical way to weight traits in breeding goal.

2 GOALS OF THE STUDY

The main goal of this work was to provide information about improving Finnish blue fox breeding. When the project started in 2002, all breeding value evaluations were done using the same single trait model. All traits were assumed to have a heritability of 0.2. The statistical model was the same for all traits. The only fixed effect was the farm*year interaction. The only random effects were additive genetic and residual. Breeding value evaluations were done within farm.

Among farmers, there was serious concern about the level of inbreeding in the Finnish blue fox population. The concern was raised by the observed poor fertility of females. One explanation for the poor fertility could be inbreeding depression. Scientific information was needed to estimate the level and rate of inbreeding in Finnish blue fox population.

In the Finnish breeding scheme a total merit index was calculated without genetic correlations between traits. Moreover, the weight of each trait in the total merit index was based on a compromise between the results obtained by studies (Lohi 2002, Lind & Lohi 1999) and from normal farm practice.

Article	Goal	Results
I	Assessment of genetic variation from pedigree	<ul style="list-style-type: none"> • Coefficients of relationship • Coefficients of inbreeding • Rate of inbreeding • Effective population size
II, III	Estimation of genetic parameters	<ul style="list-style-type: none"> • Heritabilities • Genetic correlations • Statistical models • Testing of transformed scale
IV, Thesis compilation text	Determination of economic weights, comparison of different selection strategies	<ul style="list-style-type: none"> • Marginal economic values • Number of discounted expressions • Correlated responses • Total value (EUR) of the genetic gain in breeding goal by selection strategy

Figure 5. Aims of the work.

The study goals were divided into three parts (Figure 5). The first goal (Paper I) was to estimate population parameters. The second goal (Papers II and III) estimated genetic parameters for grading traits, pelt character traits

and litter size. The third goal (Paper IV) created and used a bio-economic model to estimate economic weights for Finnish blue fox production and to compare different selection strategies from an economic point of view.

3 MATERIALS AND METHODS

3.1 MATERIALS

The data of the study are described in Figure 6. Most data were obtained from the SAMPO-register collected from Finnish fur farms by the Finnish Fur Breeder's Association.

Data for variance component analysis were sampled from the full data in an attempt to get good genetic ties between the farms. The bestconnected farms belonged to a breeding circle where males were owned jointly. Only the data from purebred blue foxes were accepted. After the data edits the analyzed data had 54680 (paper II) and 53720 (paper III) animals from 7 farms.

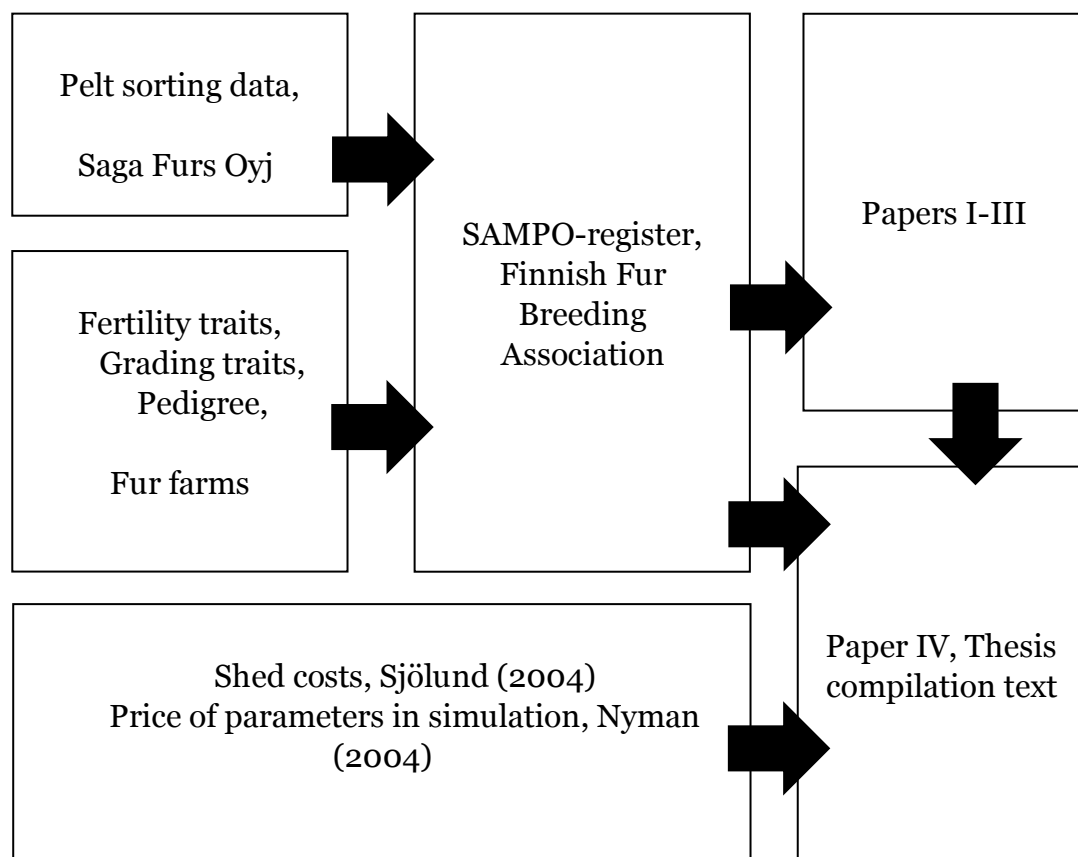


Figure 6. Source of data in the studies

In the analysis of coefficients of inbreeding and relationship (paper I) only farms with at least 50 breeding foxes annually in 5 consecutive years during 1990-2004 were accepted into the statistical analysis. Hence, the number of

animals on a farm had to be 10 or more per birth year in order to be included in the statistics. These selection criteria were fulfilled by 215 farms. The sampled farms had about 3.2 million blue foxes. The number of breeding animals was 237 487 during 1990 to 2003.

Studied traits in paper II were grading traits and pelt character traits, in paper III pelt size, litter size and age at first insemination and in paper IV grading traits, pelt character traits, litter size, pregnancy and felicity (Table 3).

Table 3. Traits studied in papers II-IV

	Genetic parameters		Economic values
	Paper II	Paper III	Paper IV
Pelt character traits			
Pelt size	X	X	X
Color darkness	X		
Color clarity	X		X
Quality	X		X
Grading traits			
Animal size	X		X
Color darkness	X		X
Color clarity	X		X
Density	X		X
Guard hair coverage	X		X
Quality	X		X
Fertility traits			
Litter size		X	X
Age at first insemination		X	
Pregnancy			X
Felicity			X

3.2 METHODS

The methods used in this thesis are presented in Table 4.

3.2.1 ASSESSMENT OF GENETIC PARAMETERS FROM PEDIGREE

In paper I, coefficients of relationship and inbreeding (Wright, 1922) were calculated.

Mean coefficients of the relationship between breeding animals, predicts the future inbreeding of the population. In this study coefficients of the relationship were calculated between males and females by birth year, and between all breeding animals by birth year.

The effective population size was calculated using

$$N_e = 1 / (2\Delta F) \quad (1)$$

Where ΔF is rate of inbreeding per generation. The existence of overlapping generations in our data was taken into account in computing the rate of inbreeding (Cutiérrrez et al. 2003).

Table 4. *Methods and software used in the thesis*

Paper	Methods / software	Reference
I	Coefficient of Relationship (α)	Wright (1922)
	Coefficient of inbreeding (F_i)	Wright (1922)
	Rate of inbreeding (ΔF)	Cutiérrrez et al. (2003), Rendel & Robertson (1950)
	Effective population Size (N_e)	Cutiérrrez et al. (2003)
II-III	Multitrait animal model, REML (DMU)	Madsen & Jensen (2000), Sorensen & Gianola (2002)
IV	Bio-economic simulation	De Vries (1989)
		Houška et al. (2004)
Thesis compilation	Number of discounted expression (NDE)	Nitter et al. (1994)
	Genetic change on traits in breeding objective (restricted and non-restricted)	Cunningham et al. (1970)

3.2.2 GENETIC PARAMETERS

Restricted maximum likelihood (REML) estimates of (co)variance components (papers II and III) were calculated with a multitrait animal model using DMU (Madsen & Jensen 2000). In papers II-III the model in the variance component estimation was:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{W}_c\mathbf{c} + \mathbf{Z}_a\mathbf{a} + \mathbf{e} \quad (2)$$

Where \mathbf{y} is vector of observations, \mathbf{b} is a vector of fixed effects, and \mathbf{c} , \mathbf{a} and \mathbf{e} are vectors of random litter, animal and residual effects. Matrices \mathbf{X} , \mathbf{W}_c and \mathbf{Z}_a are corresponding incidence matrices.

Random effects \mathbf{a} , \mathbf{c} and \mathbf{e} were assumed to be independent. In addition, $\text{Var}(\mathbf{a}) = \mathbf{G}_0 \otimes \mathbf{A}$, where \mathbf{A} is the numerator of the relationship matrix, and \mathbf{G}_0 is the additive genetic covariance matrix. In papers II and III inbreeding coefficients of all animals were assumed to be zero, whereas in paper I diagonal elements (relationship of animal to itself) in matrix \mathbf{A} were assumed to be:

$$a_{ii} = 1 + F_i \quad (3)$$

where F_i is the coefficient of inbreeding, $F_i = \frac{1}{2}a_{sd}$ and a_{sd} is the relationship of sire and dam of animal i .

Litter effects and residual effects between animals were independent but correlated within animals between different traits. Random effects were assumed to be normally distributed with mean zero.

Heritability (h^2) and proportion of litter variation (c^2) for a trait were calculated as

$$h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2) \quad (4)$$

$$c^2 = \sigma_c^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2) \quad (5)$$

where σ_a^2 , σ_c^2 and σ_e^2 are additive genetic, litter environment and residual variances for the trait, respectively.

Because of computational limitations, the estimation in paper II was divided into several analyses including 3 or 4 traits at a time. Consequently, several (co)variances were estimated for the same traits. Means of the estimates were used to calculate genetic correlations, heritabilities and their standard errors and the proportion of litter variation and their standard errors.

3.2.3 DETERMINISTIC BIO-ECONOMIC SIMULATION

In paper IV a deterministic bio-economic simulation model was created to estimate the marginal economic values of a typical Finnish blue fox farm (Figure 7). The basic structure of simulation was close to that presented by De Vries (1989), but the calculation of the marginal profit was similar to that used by Houška et al. (2004) and Wierzbicki et al. (2007). To make traits comparable each trait was multiplied by its genetic standard deviation.

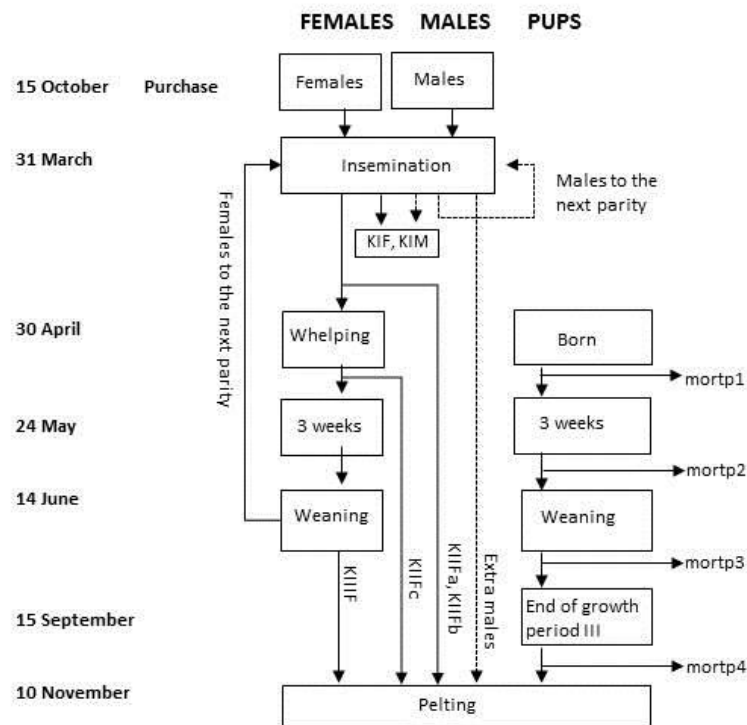


Figure 7. Course of females, males and pups life in the simulation. KIF = culling for anoestrus, KIIFa = culling for barren, KIIFb = culling for abortion, KIIFc = culling for pup killing, KIIIF = culling for other reasons, KIM = culling due to male fertility problems, Mortp1, 2, 3 and 4 = mortality percentage in growth stages 1, 2, 3 and 4.

3.2.4 COMPARISON OF THE DIFFERENT SELECTION STRATEGIES

3.2.4.1 Number of discounted expressions

The time interval between the selection and expression of the trait varies from trait to trait. Moreover, some traits can be expressed several times whereas other traits are expressed only once. The returns of selection work will often materialize much later than the associated costs. Therefore for

analyzing breeding strategies the net returns have to be discounted. In order to take into account the facts, marginal economic values of each trait were multiplied by their number of discounted expressions (NDE). The calculation of NDE was based on the gene flow method (Hill, 1974). Most traits can be divided into two groups: direct and maternal traits (Wolfová and Nitter 2004). In the present study, NDE values were calculated separately for direct traits (pelt size, quality and color clarity) and the maternal trait (litter size) using the formula used by Nitter et al. (1994):

$$NDE_g = \mathbf{q}_g' \sum_{t=1}^T \mathbf{m}_t (1+d)^{-t} \quad (6)$$

where NDE_g is the NDE for the particular trait group g ($g=1$, maternal, $g=2$, direct), \mathbf{q}_g is the realization vector for the trait group g , \mathbf{m}_t is a vector with gene proportions in all sex×age classes at time t , T is investment period and d is discount rate per year. The vector \mathbf{m}_t was calculated by

$$\mathbf{m}_t = \mathbf{Z}\mathbf{m}_{t-1} \quad (7)$$

where \mathbf{Z} is a transition matrix that describes the reproduction and survival of individuals of different age classes. In Finland, blue fox breeding is mostly done in the commercial farms, and, therefore, the structure of transition matrix \mathbf{Z} is fairly simple. The reproduction and age structure of breeding females and males were calculated from the SAMPO database (Table 5).

Table 5. Age distribution (%) for the dams and the sires of pups, sires and dams used in NDE analysis in Finnish blue fox production

year class	Pup		Sire		Dam	
	Sire	dam	sire sire	sire dam	dam sire	dam dam
1	66.00	35.00	64.17	37.71	60.04	30.39
2	24.00	28.00	22.16	34.32	24.44	33.85
3	6.00	13.00	8.00	14.92	9.43	18.64
4	3.00	10.00	3.28	7.74	3.63	10.7
5	1.00	8.00	2.39	3.61	2.26	4.56
6	-	6.00	-	1.70	-	1.86

Half of the genes are from the sire and the other half from the dam and animals maintain their genes over years.

Moreover, at year 1 vector $\mathbf{m}_1 = \mathbf{Z}\mathbf{m}_0$ which can be written:

$$\mathbf{m}_1 = \begin{bmatrix} 0.321 & 0.111 & 0.040 & 0.016 & 0.012 & 0.186 & 0.171 & 0.075 & 0.039 & 0.019 & 0.085 & 0 \\ 1.000 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1.000 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1.000 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1.000 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} 1.0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\mathbf{m}_1 = \begin{bmatrix} 0.300 & 0.122 & 0.048 & 0.018 & 0.012 & 0.152 & 0.169 & 0.093 & 0.054 & 0.023 & 0.093 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1.000 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1.000 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1.000 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1.000 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} 1.0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\begin{bmatrix} 0.330 & 0.120 & 0.030 & 0.015 & 0.005 & 0.175 & 0.140 & 0.065 & 0.050 & 0.040 & 0.030 & 0 \end{bmatrix} \begin{bmatrix} 1.0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

0.5
0.5

The \mathbf{Z} matrix has blocks that quantify gene proportions that are transmitted within and between groups and age classes of male and female breeding animals and their pups. In other words, genes in the current generation are determined by genes and age combination of dams and sires of the preceding generation (Figure 8). Because a pup does not pass any genes onto its siblings or to its parents the last column in \mathbf{Z} is all zeros.

$$\mathbf{Z} = \begin{array}{|c|c|c|} \hline \mathbf{M} \text{ to } \mathbf{M} & \mathbf{F} \text{ to } \mathbf{M} & \mathbf{P} \text{ to } \mathbf{M} \\ \hline \mathbf{M} \text{ to } \mathbf{F} & \mathbf{F} \text{ to } \mathbf{F} & \mathbf{P} \text{ to } \mathbf{F} \\ \hline \mathbf{M} \text{ to } \mathbf{P} & \mathbf{F} \text{ to } \mathbf{P} & \mathbf{P} \text{ to } \mathbf{P} \\ \hline \end{array}$$

Figure 8. Basic logic of the transition matrix \mathbf{Z} . M = Males, F = Females, P = Pups

In the present study, the investment period (T) was 10 years and the discount rate per year (d) was 3%. According to Smith (1978) a discount rate of 3% is the best estimate (a long term mean rate of interest) of the future real discount rate of investment in animal production. Too low a rate of interest may underestimate the cost of investment and would give too optimistic an estimate of future net revenues. Moreover, too high a rate of interest would give too pessimistic estimate of future revenues.

3.2.4.2 Responses of selection

In Finland breeding values are estimated for blue foxes by using single trait BLUP animal models. The economic values were not derived exactly for the evaluated traits. The breeding value evaluation does not use the known genetic correlation structure among traits. For these reasons, three sets of alternative economic weights were derived to offer multi-trait total merit indices for selection. Economic selection index weights were estimated using basic selection index formula

$$\mathbf{b} = \mathbf{V}^{-1}\mathbf{G}\mathbf{a} \quad (8)$$

where \mathbf{b} is the vector of economic selection index weights in selection criteria, \mathbf{V}^{-1} is an inverse of phenotypic co-variance matrix of observations, \mathbf{G} is genetic co-variance matrix between traits in selection criteria and breeding objective, and \mathbf{a} is the vector of marginal economic values times NDE values in the breeding objective.

Three optional selection criteria (Table 6) were compared: 1) Selection of grading traits and litter size, 2) selection of pelt character traits and litter size and 3) selection of all traits. The selection objective was always for the improvement of pelt character traits (excluding pelt color darkness) and litter size without restrictions. In addition to these, all options considered scenarios for which genetic change in pelt size was restricted to zero (Cunningham et al. 1970).

Table 6. Traits in three optional selection strategies for the Finnish blue fox

	Traits in selection criteria		
	Grading traits and litter size	Pelt character traits and litter size	All traits
Litter Size	X	X	X
Pelt character traits			
Pelt size		X	X
Color darkness		X	X
Color clarity		X	X
Quality		X	X
Grading traits			
Animal size	X		X
Color darkness	X		X
Density	X		X
Guard hair coverage	X		X
Color clarity	X		X
Quality	X		X

The economic selection index weights were derived using an assumption that single trait (animal model) BLUPs can be considered to be progeny test evaluations and the amount of information in evaluations is derived from accuracy of single trait animal model BLUP. Progeny means are used as hypothetical observations. Thus, assume that each phenotypic observation is a progeny test index for trait i given by

$$Y_i = \beta_i (\overline{Y_{n_h}} - \mu) \quad (9)$$

where μ is the population mean and $\overline{Y_{n_h}}$ is the mean of progeny and β_i is the regression of breeding value of progeny mean with the value

$$\beta_i = \frac{n_h}{n_h + \lambda_i} \quad (10)$$

where n_h is hypothetical number of progeny with records and λ_i is the ratio of residual variance and progeny test variance. In the sire model

$$\lambda_i = \frac{(4 - h_i^2)}{h_i^2} \quad (11)$$

where h_i^2 is heritability for trait i . Given that the hypothetical progeny means as observations phenotypic co-variance matrices were created for all three cases (Table 6). The first step was to calculate hypothetical number of daughters for each trait with given mean reliability (r_i^2) of breeding values. Reliabilities were obtained from SAMPO data using only the information that was assumed to be available at the moment of selection.

For each trait the hypothetical number (n_h) of progeny with observations was calculated using a procedure used for dairy cattle breeding. Interbull calculates the equivalent daughter contributions (EDC) in order to be able to estimate internationally comparable total merit indices for bulls (Fikse & Banos 2001). Because the squared correlation between breeding value and progeny mean is equal to the regression coefficient given by (10) EDC or in our case, the hypothetical number of daughters with observations for trait i can be calculated using the variance ratio and reliability:

$$n_h = \frac{\lambda_i r_i^2}{1 - r_i^2} \quad (12)$$

For a trait combination such a hypothetical number of daughters can be recreated using equation:

$$n_{h_{ij}} = p(n_{h_i} + n_{h_j}) \quad (13)$$

$$\text{where } p = \frac{n_{ij}}{n_{ij} + 1} \quad (14)$$

with

$$n_{ij} = \frac{n_{ij}}{n_i + n_j - n_{ij}} \quad (15)$$

where n_i , n_j and n_{ij} are mean numbers of daughters with observations in trait i and j and their combination in real SAMPO data, respectively.

Before creating genetic and phenotypic (co)variance matrices, true phenotypic (co)variance matrices \mathbf{P} residual (co)variance \mathbf{R} were created. Variances and covariances for the matrix were collected from the analysis of papers I and II. After that the matrix was forced to be positive-definitive using bending procedure described by Hayes & Hill (1981). Next genetic co-variance matrix \mathbf{G} was estimated as follows

$$\mathbf{G} = 0.25 * \begin{bmatrix} h_1 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & h_w \end{bmatrix} \begin{bmatrix} \sigma_{P_1}^2 & \dots & \sigma_{P_{1w}} \\ \vdots & \ddots & \vdots \\ \sigma_{P_{w1}} & \dots & \sigma_{P_w}^2 \end{bmatrix} \begin{bmatrix} h_1 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & h_w \end{bmatrix} \quad (16)$$

where $h_i = \sqrt{h_i^2}$. Moreover, genetic correlation is assumed to equal phenotypic correlation. $\sigma_{P_i}^2$ is phenotypic variance for trait i , and $\sigma_{P_{ij}}$ is phenotypic covariance between traits i and j . Here, constant 0.25 is coefficient of relationship between parent and offspring. The phenotypic (co)variance matrix for the source of information in the selection index was calculated with

$$\mathbf{V} = \begin{bmatrix} \sigma_{P_i}^2 & \dots & \sigma_{P_{1w}} \\ \vdots & \ddots & \vdots \\ \sigma_{P_{w1}} & \dots & \sigma_{P_w}^2 \end{bmatrix} = \begin{bmatrix} r_1^2 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & r_w^2 \end{bmatrix} \begin{bmatrix} \sigma_{P_{1(h)}}^2 & \dots & \sigma_{P_{1w(h)}} \\ \vdots & \ddots & \vdots \\ \sigma_{P_{w1(h)}} & \dots & \sigma_{P_{w(h)}}^2 \end{bmatrix} \begin{bmatrix} r_1^2 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & r_w^2 \end{bmatrix}$$

(17)

where

$$\sigma_{P_{i(h)}}^2 = \sigma_{G_i}^2 + \frac{\sigma_{R_i}^2}{n_h} \quad (18)$$

$$\sigma_{P_{ij}} = \sigma_{P_{ji}} = \sigma_{G_{ij}} + \frac{\sigma_{R_{ij}}}{n_{h(ij)}} \quad (19)$$

where $\sigma_{R_i}^2$ is residual variance of trait i and $\sigma_{R_{ij}}$ is residual covariance between trait i and j .

The response of selection in traits in breeding objective was estimated using

$$\mathbf{s} = \frac{\mathbf{b}'\mathbf{G}}{\sqrt{\mathbf{b}'\mathbf{V}\mathbf{b}}} \quad (20)$$

where \mathbf{s} is the vector responses in original units for each trait in the selection objective. The economic total value in selection objective in different selection strategies was calculated using:

$$EUR = \sqrt{\mathbf{b}'\mathbf{V}\mathbf{b}} \quad (21)$$

4 RESULTS

4.1 STATE OF GENETIC VARIATION

Finnish fox farmers usually do not mate animals that have common parents or grandparents. This relatively simple safeguard has been an effective way to avoid increase in inbreeding.

The mean coefficient of inbreeding was low (Paper I, table 1). In general, the coefficients of inbreeding were lower among breeding animals than among all animals. For animals in production and not used for breeding purposes, it may in some cases be even beneficial to mate close relatives. This might be a good way to get genetic advance in some good characteristics.

Inbreeding seems not to be a problem in the Finnish blue fox population. As much as 68% of the studied farms had mean inbreeding less than 1%. Only 5 farms had mean inbreeding above 3%.

However, the level of inbreeding at one particular moment is not important. The level of inbreeding for a certain moment is determined mainly by length of pedigree used in the analysis. What is more important is to know the rate of inbreeding in the population.

The rate of inbreeding by generation was estimated to be from 0.107% to 0.191% depending on the year in question. However, some mild bottlenecks can be seen in the population. The seasons 1998 and 1999 were economically difficult for fox farmers. For this reason, the number of breeding animals was decreased and only the best were kept over winter to be ready for the spring mating season.

The effective population size was 459 when estimated from the whole data. The data from 1998 to 2003 indicated that the effective population size decreased to 258. This is due to the slight bottleneck at the end of 1990 s. Even though the effective population size was smaller with subset data, it is still relatively high when compared to studies made on other species (Cutiérréz et al. 2003; Woolliams & Mäntysaari 1995).

The generation interval was estimated to be 1.59 years from males to breeding males, 1.64 years from males to breeding females, 2.12 years from females to breeding males and 2.34 years females to breeding females. The mean generation interval was 1.92 years.

The annual rate of inbreeding was estimated to be from 0.059% to 0.100% depending on the considered years (Paper I, table 2). There was hardly any change between 1990 and 1997. Furthermore, the mean coefficient of relationship increased faster during 1998 and 1999 for the reason described above. It is commonly known, that the more intense the selection is, the closer the relatives the selected animals tend to be.

4.2 GENETIC PARAMETERS

The phenotypic variation, the proportion of variation due to common environment (litter) and the heritabilities for studied traits are presented in Table 7 (Papers II & III). Color darkness had the highest heritability. In general, pelt character traits had higher heritabilities than grading traits. Heritability of litter size was low.

Table 7. Phenotypic variation and proportion of litter variation and heritability (Papers II and III) in pelt and fertility traits of blue foxes

	Coefficient of variation	Phenotypic variation	Proportion of variation	
			Common environment (c²)	Heritability (h²)
Pelt traits (scale 1-5)				
Size¹	0.26	0.51	0.08	0.30
Size, transformed scale²	0.41	5906	0.09	0.29
Color Darkness³	0.51	1.33	0.05	0.55
Color Clarity³	0.20	0.48	0.08	0.16
Quality³	0.15	0.35	0.06	0.22
Grading traits (scale 1-5)				
Size³	0.11	0.23	0.07	0.16
Color Darkness³	0.22	0.35	0.10	0.51
Color Clarity³	0.11	0.23	0.13	0.10
Density³	0.15	0.36	0.11	0.15
Guard hair Coverage³	0.13	0.31	0.10	0.19
Quality³	0.13	0.28	0.12	0.11
Fertility traits				
Litter size, 1 st parity²	0.49	7.96	0.01	0.10
Litter size, 2 nd parity²	0.38	10.49	0.09	0.06
Age at first insemination², d	0.04	78.10	0.08	0.29

¹Mean of papers II and III. ²Paper III, ³Paper II. Standard errors of proportion of common environment variation and heritabilities were at maximum 0.02 (except 0.03-0.05 for litter size)

Significant genetic correlations are presented in Table 8 (papers II & III). The highest genetic correlations were found between pelt and animal sizes, between pelt and grading darkness, between pelt quality and grading density, between grading density and grading guard hair coverage and between grading density and grading quality. The high genetic correlations between grading density, grading guard hair coverage, grading quality and pelt quality indicate that grading traits are an effective way to improve pelt quality.

There were only few antagonistic genetic correlations between the studied traits. Highest antagonistic correlation was between pelt size and litter size, and between grading size and grading color clarity. Animal and pelt size had many favorable correlations with fur quality traits.

An alternative transformation scale for pelt size was tested in paper II. The proportion of pelts in the largest size class had increased substantially and after 1999 new size classes for large pelts had not been introduced. However, even though the coefficient of variation (CV) was higher with transformed scale (Table 7), the effect of transformation on genetic parameters and genetic trends was negligible.

Table 8. Genetic correlations with absolute values higher than $1.96 \times SE$ between grading traits, pelt character traits and litter size (LS) (Papers II and III) in Finnish blue foxes

Pelt	Pelt Character traits				Grading Traits						
	Size	Dark	Cla	Qua	Size	Dark	Cla	Den	Cov	Qua	LS
Size				+	+++	+		++	+	++	--
Darkness			+	+	-	+++	+	-	++		
Clarity				+			+				
Quality					++	+	+	+++	++	++	
Grading											
Size							--	++		+	
Darkness									++	+	
Clarity									++	++	
Density									+	+++	
Guard hair coverage										+++	
Quality											
Litter size											

+ favorable correlation, - antagonistic correlation. One symbol: $0.10 < |r_g| < 0.20$, two symbols: $0.20 < |r_g| < 0.70$, three symbols: $0.70 < |r_g|$

4.3 DETERMINISTIC BIO-ECONOMIC SIMULATION

4.3.1 INTERMEDIATE RESULTS

The deterministic bio-economic simulation produced a lot of information about blue fox production in general. The production and pup losses within different production stages are presented in Figure 9.

Even though the number of females and the total number of pups born are highest in the youngest female class, the total production (pelt produced)

is actually smaller than among 2-year old females. This is due to high pup losses during gestation and before weaning of the 1-year old females.

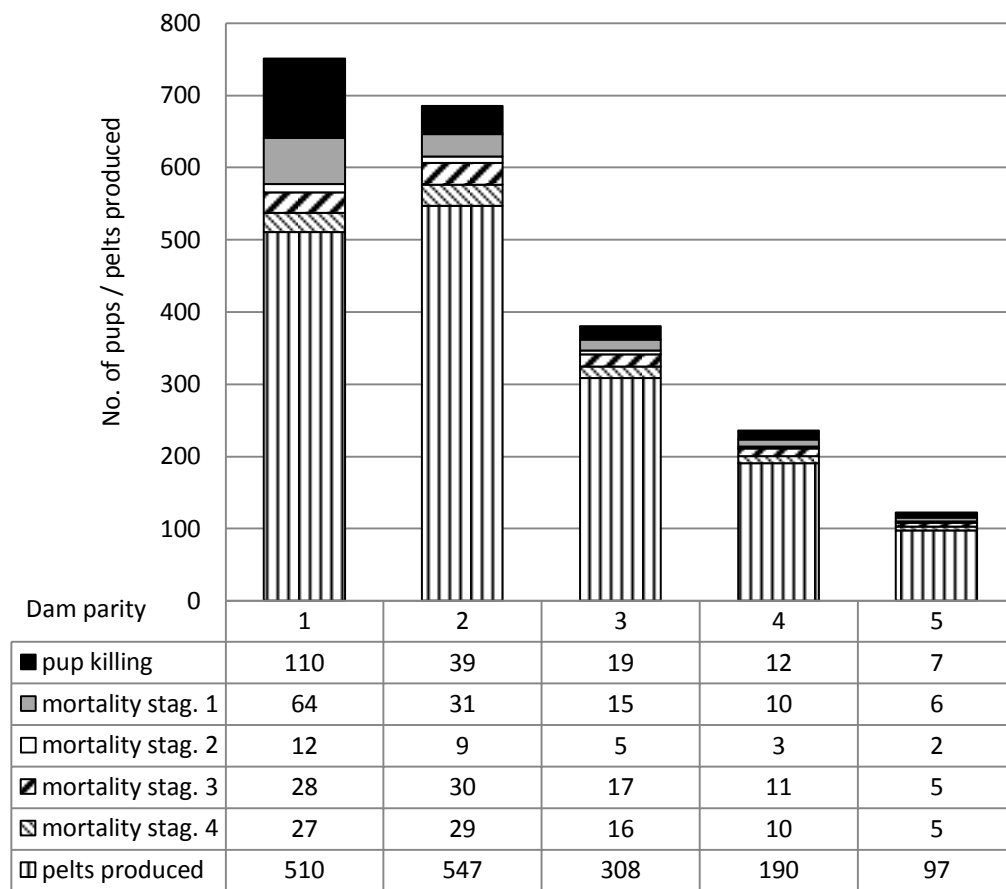


Figure 9. The numbers of pelt produced and mortalities in different production stages of pups from dams across parities 1 to 5 (paper IV) in the Finnish blue fox: represented with the age distribution and reproduction of a typical farm with 338 females.

4.3.2 MARGINAL ECONOMIC VALUES

Pregnancy and felicity clearly had the highest economic values and economic weights (Table 8, paper IV). Because of the binary nature of these two traits, the genetic variation is extremely small for both traits. When genetic variation was taken into account, litter size had almost as high marginal economic value as felicity and pregnancy. Pelt size has the second highest marginal economic value. The economic value of pelt color clarity was very small.

Changes in feed price, pelt price or litter size had only minor effects on relative economic weights of the traits. Usually, when environmental circumstances change in a worse direction, the relative economic weight of pelt quality increases.

4.4 COMPARISON OF DIFFERENT SELECTION STRATEGIES

4.4.1 NUMBER OF DISCOUNTED EXPRESSIONS

Table 9 includes values from formula (6), which were used in the calculation of NDE in year 10. The NDE value for direct traits (pelt character traits) is 3.56 and that for maternal trait (Litter size) is 3.46.

Table 9. Values of components of formula used in the calculation of NDE at T=10

	Year	Realization vectors		$\sum_{t=1}^T \mathbf{m}_t(1+d)^{-t}$
		Maternal (\mathbf{q}_1)	Direct (\mathbf{q}_2)	
Sire	1	0	0	3.62
	2	0	0	4.05
	3	0	0	3.56
	4	0	0	3.09
	5	0	0	2.66
Dam	1	0.35	0	3.56
	2	0.28	0	3.98
	3	0.13	0	3.50
	4	0.10	0	3.04
	5	0.08	0	2.61
	6	0.06	0	2.20
Pup	1	0	1	3.56

Table 10. Marginal economic value (MEV), genetic standard deviation (σ_g), number of discounted expressions (NDE) and economic weight (EW) of the traits in the breeding programme of the Finnish blue foxes

	MEV (EUR)	σ_g	NDE	EW
Litter size	22.95	0.80	3.46	63.5
Pregnancy	329.03	0.06	3.46	68.3
Felicity	335.90	0.08	3.46	93.0
Pelt size	13.18	0.40	3.56	18,8
Pelt quality	25.59	0.28	3.56	25.5
Color clarity	1.17	0.28	3.56	1.2

MEV = Marginal economic value (paper IV), σ_g = genetic standard deviation (papers II-III),

NDE = Number of discounted expressions, EW = economic weight = MEV x σ_g x NDE.

Table 10 has economic values multiplied by NDE-values. Compared to the results presented in paper IV (Paper IV, table 7.), NDE-values did not change the order of the traits in terms of their economic value.

4.4.2 ECONOMIC SELECTION INDEX WEIGHTS IN DIFFERENT SELECTION STRATEGIES

Table 11 shows the economic selection index weights for three different selection strategies. In the first case, selection criteria include litter size and pelt character traits. In this case the highest weight (42.8%) was found for pelt quality. The second highest was estimated for litter size (35.3%) and third highest for pelt size (18.3%).

Table 11. *Relative economic selection index weights for traits in selection objective in three different selection strategies in non-restricted (free) and restricted (restr) cases of Finnish blue foxes*

	Litter size+Pelt		Litter size+Grading		All	
	Free	Restr.	Free	Restr.	Free	Restr.
Litter Size	35.3	45.0	49.0	59.1	28.6	32.3
Pelt character traits						
Pelt size	18.3	-1.2	-	-	10.9	1.1
Color darkness	0.8	1.0	-	-	0.1	0.8
Color clarity	12.8	2.7	-	-	1.4	1.4
Quality	42.8	50.2	-	-	30.8	34.2
Grading traits						
Animal size	-	-	-2.4	-3.4	11.7	-3.7
Color darkness	-	-	17.7	1.9	4.0	4.2
Density	-	-	3.5	3.8	12.1	8.8
Guard hair coverage	-	-	6.4	1.3	-0.2	-1.9
Color clarity	-	-	11.7	1.5	-0.2	7.5
Quality	-	-	9.4	19.2	-0.3	-4.0

When the genetic change in pelt size was restricted to zero, the weight of pelt quality increased up to 50.2%. Hence, the weight for pelt size became slightly negative. The economic selection index weight for color clarity in the unrestricted case was 12.8%, whereas in the restricted case it was only 2.7%. The economic selection index weight for color darkness was small in both cases.

In the second case, selection strategy, selection criteria included litter size and grading traits. Approximately half of the weight was assigned to litter size (49.0% and 59.1% in the unrestricted and restricted cases, respectively).





Among grading traits, the highest weight was given to grading pelt darkness in the unrestricted case (17.7%) and to pelt quality in the restricted case (19.2%).

In the third case, all traits were included in the selection criteria. The highest weight (30.8% and 34.2% in the unrestricted and restricted cases, respectively) was estimated for pelt quality. The second highest weight was given to litter size and third highest to grading density.

4.4.3 CORRELATED RESPONSES AND TOTAL VALUE OF GENETIC GAIN

Table 12 has genetic change in traits in selection objective when the total merit index in selection criteria was changed by one standard deviation unit. The changes in traits in selection criteria were presented both in original units and in genetic standard deviation units. Different selection strategies had only minor effects on the genetic change in litter size. In all restricted cases the genetic change in pelt size was naturally zero. Color clarity seemed to benefit most from the selection strategy based on litter size and grading traits.

Table 12. Genetic change in litter size (LS), pelt size, color clarity and quality in different selection strategies presented in original units (ΔG) and in standard deviation units ($\Delta G/\sigma_g$) and total value (€) of the change in three selection strategies both in free and restricted scenarios for one standard deviation change in the total merit index.

	LS		Pelt size		Color clarity		Quality		
		$\frac{\Delta G}{\sigma_g}$		$\frac{\Delta G}{\sigma_g}$		$\frac{\Delta G}{\sigma_g}$		$\frac{\Delta G}{\sigma_g}$	€
Free									
LS+Pelt	0.05	0.06	0.02	0.04	0.00	0.00	0.00	0.00	1.697
LS+Grad	0.05	0.06	0.02	0.05	0.02	0.07	0.00	0.00	1.562
All	0.04	0.05	0.04	0.09	0.00	0.01	0.02	0.08	1.915
Restricted									
LS+Pelt	0.06	0.07	0.00	0.00	0.00	0.00	0.01	0.05	1.581
LS+Grad	0.06	0.08	0.00	0.00	0.02	0.07	0.00	0.01	1.487
All	0.06	0.07	0.00	0.00	0.00	0.00	0.02	0.07	1.698

The total value of genetic change was highest (1.915 EUR) when selection criteria included all traits without restrictions. Selection strategy based on litter size and pelt character traits yielded higher economic benefit than strategy based on litter size and grading traits. In general, when genetic

change in pelt size was restricted to zero, the total value of economic change was lower than in unrestricted cases. However, the differences to unrestricted cases were small. The poorest selection strategy from the economic point of view seem to be selection based on litter size and grading traits when genetic change in pelt size was restricted to zero.

5 DISCUSSION

5.1 MAIN RESULTS AND QUALITY OF THE DATA

The main results of this thesis were 1) Genetic variation of the Finnish blue fox population is sufficient and inbreeding is not a problem in the current population, 2) The heritabilities of the traits in Finnish blue fox breeding vary from 6-10% for fertility traits and 10-55% for pelt traits, 3) The genetic correlation of blue fox size has an antagonistic genetic correlation with litter size, 4) Litter size has the highest economic value and weight in the Finnish blue fox breeding scheme and 5) Genetic change of pelt size can be restricted to zero without major economic losses being incurred.

The SAMPO-data used in this thesis (Papers I, II and III) was clearly larger (approximately 45 000 observations in pelt character traits, 8000 observations in grading traits and 5500 observations in litter size) than in any previous studies on blue foxes. The dataset selected for the analysis had good genetic ties between the farms. However, the identification system for the animals had been created solely for the purpose of within farm use. Therefore, foxes bought from other farms had different ID-number in different farms. In such cases ID-numbers had to be considered as siblings instead of the same individual.

The measuring system used by Saga Furs for pelt size, color darkness and color clarity are extremely high quality systems. However, a large amount of information is lost when each measurement, especially pelt size, is transformed to the auction house classes (Table 1) instead of using original measurements. This decreases genetic variation artificially. This is irrational from the animal breeding point of view and it decreases the opportunities to achieve genetic change in breeding scheme.

5.2 STATE OF VARIATION IN THE FINNISH BLUE FOX POPULATION

The Finnish blue fox population was estimated to have a relatively large effective population size. This supports the conclusion that there has not been any major “bottlenecks” in the population over the pedigree recording period. This study clearly suggested that inbreeding in general is not a problem in the Finnish blue fox population. The mean coefficient of inbreeding and the mean rate of inbreeding were low.

Blue foxes are seasonal breeders. This is the main reason why a central artificial insemination center has not been established for blue fox

production in Finland. Most farmers use their own males for impregnating females, therefore pedigree connections between farms are very sparse.

When the selection of males is carried out on the farm and is also based on the information available within that farm, the selection differential cannot be very high. Hence, there is also a risk of genetic drift within the farm. On the other hand, in this kind of population structure, the purchase of new breeding animals is an effective way to decrease inbreeding and achieve favorable heterosis on any farm that has some inbreeding.

It is likely, that many farmers do not understand what inbreeding actually is. Inbreeding is not a feature that will accumulate when an inbred animal is moved from farm to another, if there are no genetic links between the two farms. Moreover, the fear of inbreeding depression is often exaggerated. Inbreeding depression can be seen only with relatively high, 10% or more inbreeding levels (Nordrum 1994), which is rare in the Finnish blue fox population. It is much more important to minimise the rate of inbreeding or maximize the effective population size to keep the genetic variation as wide as possible.

5.3 SELECTION POTENTIAL IN THE FINNISH BLUE FOX POPULATION

5.3.1 GENETIC BACKGROUND OF THE TRAITS IN THE BREEDING GOAL

Heritabilities of the traits in the breeding objective (pelt character traits and litter size) varied from low to moderate. Litter size had the lowest heritability, which agrees with other studies (Wierzbicki 2004 & Koivula et al. 2009).

Correlations between the grading traits and the pelt character traits were assumed to be high. However, the correlation between density and guard hair coverage with pelt quality was unknown prior to this study. This paucity of information was mainly due to a difficult definition of pelt quality.

As described before, pelt quality is a complex combination of under fur density, length and quality and guard hair length, smoothness and quality. Hence, either good under fur or good guard hair do not necessarily guarantee high pelt quality. Moreover, their combination is very important.

Because pelt quality is such a complex trait, it makes sense, that farmers focus on grading details, which seem to predict pelt quality. However, it is important to know the genetic correlations between these quality measurements in order to achieve highest possible economic benefit.

Animal size combined with pelt size, and pelt color darkness combined with grading color darkness, were highly genetic correlated for live animal grading and pelt grading. They are all easy to measure. Color clarity is a

difficult trait to measure in farm conditions. The genetic correlation between pelt color clarity and grading color clarity was low.

The genetic correlation between pelt quality and grading quality was lower than the genetic correlation between pelt quality and grading density. This indicates that to some extent the farmers pay attention to other things in grading than the professional graders in the auction house. Density is a trait, which corrects some deficits in guard hair coverage. If guard hairs are weak, high density can still give at least a satisfactory pelt quality. However, there is concern among professional graders that too high a density may lead to unwanted woolliness, where hairs might get tangled.

5.3.2 PROBLEMATIC TRAIT COMBINATIONS

Pelt size and animal size have an antagonistic genetic correlation with litter size and some other traits. Consequently, Finnish blue fox production has struggled with unwanted genetic change in litter size in the population for several years.

The mean pelt size has increased relatively fast for several years. At the same time the mean weight (Peura 2004) and proportion of animals with leg problems (Kempe et al. 2010) have increased and the mean litter size has decreased (Bengts 2008) dramatically. The change may not be completely due to heavy selection of pelt size. Feed content has also changed (Paper II). According to the Feed laboratory of Finnish Fur Breeders Association, the proportion of fat in metabolic energy in the feed of fur animals has increased approximately 9.3 kcal per kg dry matter per year (Finsk Pälstidskrift 1994-2004). This is mainly due to tightened environmental regulations concerning the amounts of phosphorous in the manure of fur animals.

The main problem facing the Finnish blue fox breeding is obesity during the first autumn of the animal's life. Fox farmers have effectively utilized blue foxes natural genetic potential to accumulate fat under their skin during autumn. A fat fox has a large skin (Kempe et al. 2009), which again guarantees higher prices in fur auctions. However, fat animals have difficulties in coming into heat properly in the spring. They also have problems in maintaining gestation.

Because fat animals are poor producers from a fertility point of view, selected breeding animals have to go through a severe weight loss before the mating season begins. According to Koskinen et al. (2011) young females with high weight losses before the mating season also have the poorest fertility results in the ensuing mating season. However, very little is known about the biological mechanism behind this.

5.4. ECONOMIC REASSESSMENTS OF BREEDING STRATEGY

5.4.1. ECONOMIC VALUES OF THE TRAITS IN THE BREEDING SCHEME

Before this study, very little was known about the economic value of the traits of the breeding goal in the Finnish blue fox population. As pointed out earlier, large animals have larger pelts and large pelts are more valuable.

However, selection for a large pelt size has led to fatter and heavier foxes. Fat foxes also have a high capacity for dry matter intake (Kempe et al. 2010). Larger foxes consume more feed, which again increases costs per pelt produced. This study was the first attempt to take into account the increased costs due to larger pelts. Due to the increased feed costs, the economic value of pelt size was not as high as expected.

The results clearly showed that fertility and pelt quality are the most valuable traits in the Finnish blue fox production. This manifests in the poor reproduction results of one-year-old females. One-year-old females have to undergo severe weight loss before the mating season. On the other hand, the high economic value of fertility and pregnancy especially indicate the dam's suboptimal ability to maintain pregnancy and keep its pups alive before weaning. The intermediate results especially highlight poor productivity of young females.

Litter size is realized several times during the female's life. On the other hand, the blue fox produces only one pelt during its lifetime. The number of discounted expressions takes into account that some traits can be realized several times during the animal's production life. It also takes into account that the value of the trait declines, the later its realization is after the moment of selection. However, in this study the effect of the number of discounted expressions was small. This is mainly due to relatively simple production structure of blue fox production. For example, in pork production, where production is divided into several production layers (breeding units, multiplier units and commercial units), the flow of genetic material from breeding units to commercial units takes a lot more time (Houška et al. 2004).

5.4.2. OPTIMAL USE OF INFORMATION AVAILABLE

In practice, animal breeders have to compromise between the generation interval, the accuracy of breeding values of selected animals and the selection intensity. In blue fox breeding, economically the most important traits are litter size, pelt quality and pelt size. None of these traits can be measured from the animal itself when they are considered as breeding candidates. The

most important source of information that predicts litter size is the dam of the candidate.

The selection for pelt character traits is more complicated. The breeding candidate does not have a measurement of the trait and in most cases neither do the parents of the candidate. Hence, pelt character measurements of old breeding animals are not completely the same as those measured from young animals. Old animals tend to have a poorer pelt quality than young animals.

Information for breeding values of selection candidates comes mainly from half sibs from the dam's previous litters. Information from full siblings from the same litter will not be available at the time of the selection.

Grading traits can be used in animal breeding to improve pelt character traits. However, genetic correlations between grading traits and pelt character traits are less than one, as pointed out in paper II. Hence, the use of grading traits to improve pelt quality is indirect and is also less accurate.

This study showed that selection based on all traits gives only slightly better economic results than selection based only on pelt character traits and litter size. Moreover, breeding animals should not be selected only by the breeding values of grading traits and litter size.

This study also showed that the selection of breeding candidates can be optimized so that genetic change in pelt size is restricted to zero without major loss in economic value of the genetic change. However, economically the best result is achieved when no restriction is imposed. In all cases the highest marginal economic value and also the highest economic weights were given for fertility traits.

6. CONCLUSIONS

6.1. SIGNIFICANCE OF THE STUDY FOR THE FUR INDUSTRY

This study was the first study in which all the important parameters of the entire current breeding scheme for Finnish blue fox were studied. Before this study there was no information available about what is the most economic approach to weight the traits in the Finnish breeding scheme. This study also provided tools to weight traits optimally so that genetic change in pelt size is restricted to zero.

The population studies of this thesis also give important information about population structure in the Finnish blue fox population. The results highlight, that inbreeding is not a current problem in the population. However, they showed that due to occasional strong market trends, genetic “bottle necks” maybe created in the population via an over reliance on some very popular breeding animals. Hence, some farms may need to be more careful in managing their breeding animals in order to avoid losses of variation and inbreeding.

The results of this study have been taken into use between 2004 and 2006. The breeding value evaluation of the Finnish blue fox population was updated based on the statistical models and genetic parameters of this study.

Earlier breeding value evaluations were based on single trait evaluations. The first multitrait evaluation was taken into use in 2010. In 2005, the Finnish breeding program SAMPO was taken into use also Norwegian fur farms. Consequently, the results of this study are in use also in Norway.

This study was the first to estimate economic values for Finnish blue fox production. The preliminary results of this study were taken into use as early as 2006, when the Finnish Fur Breeder’s Association issued official recommendations to fur farms about economic weights on farm level breeding scheme.

6.2. FUTURE DEVELOPMENTS

Fur animal breeding faces many challenges in the future. There are some pressing environmental and animal welfare questions that need to be focused even more upon in the future. There are also some smaller scale issues that need attention. One of them is how to measure the traits in a breeding scheme. The traits in blue fox breeding are slightly problematic.

As was pointed out in paper IV, pregnancy and felicity have high economic value. However, both traits are binary traits. Consequently, more

studies are needed to investigate how the use of underlying scale would affect the results.

The most important practical tool in breeding of fertility in the Finnish blue fox is the litter result. The litter result is a problematic trait, because it also includes females with zero pups at three weeks after whelping. The almost normally distributed trait has high peak at zero. Moreover, the other fertility trait, litter size at birth, does not take into account females that have no pups three weeks after whelping.

Pelt traits are currently treated as continuous traits in blue fox breeding. However, by excluding pelt size, the true nature of these traits is not continuous. In this thesis a transformed scale for pelt size was tested but the effect was found to be negligible. More studies are needed on how similar transformations would affect genetic parameters and genetic trends of other pelt traits.

Finnish blue fox breeding has always been carried out within individual farms. Males have predominantly been used within each farm. The only exceptions to this are some breeding circles, whereby several farmers jointly own and use top sires.

Because of this practice, identification coding was created for within farm use. Consequently, animals used in several farms may have different ID numbers in different farms.

Finnish blue fox breeding is about to commence with the national breeding value evaluation. This enables higher accuracy of predicted breeding values especially within breeding farms, which sell breeding animals to other farms and farms that share males. The national breeding value evaluation also enables the use of solutions of fixed effects (such as farm-year effect) in the management of farms. It demands the uniform ID-numbering for fur farms.

Although the rate of inbreeding is not a problem in the current blue fox population, it will need more attention in the future. Due to the national evaluation scheme, the selection of males will become more effective but this entails a risk that some particular families will become very popular in the future. To avoid this, the use optimal genetic contribution theory (Meuwissen 1997; Meuwissen and Sonesson 1998; Berg et al. 2006; Sørensen et al. 2008) should be considered for blue fox breeding.

The national breeding value evaluation will probably improve in blue fox breeding history. However, the main unsolved issue in the current blue fox breeding program is fatness of the foxes and its adverse effects on leg problems, fertility and on animal welfare in general.

In nature, the blue fox has the ability to deposit fat under its skin as an energy store to survive over the winter. Natural selection favors foxes, which can store large amounts of fat during the autumn. However, in farm conditions this has conflicting outcomes. It has a clearly positive effect on pelt size but on the other hand it has several negative effects on the welfare of foxes. In most swine breeding schemes the most important trait is feed

efficiency (feed or dry matter intake / kg growth). It is usually selected along with daily gain and high carcass meat percentage (Sevón-Aimonen et al. 2007). When combined these traits ensure effective, muscular and fast growing pigs. Kempe et al. (2013) reported 0.36-0.70 genetic correlations between daily gain, feed efficiency and pelt size of blue foxes.

However, in blue fox breeding the goal is more complex than in swine since the production of meat is not the goal. Instead, the main product and goal is pelt: thus the larger the pelt, the higher its value. Nonetheless, pelt size and feed efficiency have a favourable genetic correlation current knowledge cannot answer the question: What do we actually select for when we select for feed efficiency in blue foxes? Is it possible, that the selection of the feed efficiency is actually selection of foxes are efficient at producing fat instead of muscle or bone tissue? Hermes et al. (1999) found high positive genetic correlation (0.54-0.56) between backfat depth and feed intake and no genetic correlation between muscle depth and feed intake in pigs. If that is also the case for blue foxes, then the selection for feed efficiency may lead to even more obese foxes and to worse leg and fertility problems.

One solution could be to include fat content of the carcass as a trait into a breeding scheme. However, that highlights a second question: If the selection of high fat content is more economic than production of muscle or bone tissue, why should not fur farmers select it? Should fur breeders focus more on the problem itself (fertility traits and leg weakness) instead of focusing on solving the fatness problem?

The Finnish blue fox breeding scheme needs to be put under serious scrutiny about what are the main problems in the breeding scheme and how those problems could be solved in the most economical and ethical way. Introducing new traits that focus on problematic areas of the population would probably give the best results. Clearly more efforts are also needed for the selection of fertility traits. Short-sighted selection for only pelt size alone, leads to ineffective production with welfare problems.

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